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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* × *Stellula calliope* and the possible effects of egg volume on hybridization potential

Gary R. Graves and Nancy L. Newfield

(GRG) Department of Vertebrate Zoology, National Museum of Natural History, Washington, D.C. 20560, U.S.A.; (NLN) Casa Colibrí, 3016 45th Street, Metairie, Louisiana 70001, U.S.A.

Abstract.—Plumage pattern, plumage color, and external morphology of two specimens of hybrid hummingbird (*Calypte anna* × *Stellula calliope*) are described. The parental species differ substantially in size, and the hybrids are similar to the averages of character means of the parental species. Expression of parental plumage characters in the hybrids varies, particularly the color and configuration of the frontlet and gorget. The possible effects of egg volume on hybridization potential are discussed.

The possibility of hybridization among North American species of hummingbirds (Trochilidae) was mentioned by Jeffries as early as 1888. The first published notice of such hybridization was buried in Fisher's monograph on Death Valley birds (1893), and Suchetet (1896) did not list any hybrid Trochilidae in his review of avian hybrids. Subsequently, a few additional cases were reported (e.g., Thayer & Bangs 1907, Berlioz 1930), but Banks & Johnson (1961) were the first to evaluate critically the known hummingbird hybrids from North America. The latter authors, in an exemplary study that set the standard for future work on this subject, documented five hybrid combinations based upon the direct examination of specimens and noted three other probable combinations for which they were unable to locate the pertinent specimens. Additional hybrids were reported by Short & Phillips (1967), Lynch & Ames (1970), Wells et al. (1978), and Newfield (1983). To date, a total of 13 hybrid combinations (Table 1) have been documented by specimens among the hummingbird species that regularly breed north of Mexico.

On 19 June 1926, Chester C. Lamb collected an adult male hummingbird in the Sierra San Pedro Martir (7500 ft elevation [2287 m]), Baja California del Norte, Mexico. Grinnell (1928:134) noted that Lamb's specimen (Museum of Vertebrate Zoology [MVZ], University of California No. 47983; 3.1 g), "... shows hybrid origin, apparently *Stellula calliope* × *Calypte anna,*" but left Berlioz (1930) to describe it formally. Three decades later, Banks & Johnson (1961) reexamined the specimen and elaborated on Berlioz's description. Neither Berlioz nor Banks and Johnson discussed alternative parental hypotheses.

A second hybrid hummingbird, also possibly *Calypte anna* × *Stellula calliope,* recently was collected by Newfield in Baton Rouge, Louisiana, on 22 December 1993 (Louisiana State University Museum of Natural Science, Louisiana State University (LSUMZ) No. 154189; testes minute, skull 10% ossified, light neck molt, 3.7 g, light fat, insect parts in stomach, frozen tissue saved (B-19447), prepared by Steven W. Cardiff).

Here we present a hybrid diagnosis of the two specimens and discuss the field identification of hummingbird hybrids. Finally, we briefly address the possible constraints

Table 1.—Hybrids reported among species of hummingbirds that breed north of the Mexican-U.S.A. border. References indicate the earliest publication of the identification of hybrid parentage that is currently accepted.

Hybrid combination	References
Amazilia violiceps x *Cynanthus latirostris*	Griscom 1934
Archilochus alexandri x *Calypte anna*[a]	Thayer and Bangs 1907
Archilochus alexandri x *Calypte costae*	Fisher 1893
Archilochus alexandri x *Selasphorus platycercus*[a]	Banks and Johnson 1961
Archilochus alexandri x *Selasphorus sasin*	Lynch and Ames 1970
Calypte anna x *Calypte costae*	Wells et al. 1978
Calypte anna x *Selasphorus sasin*[a]	Thayer and Bangs 1907
Calypte anna x *Stellula calliope*[a]	Grinnell 1928
Calypte costae x *Selasphorus platycercus*	Huey 1944
Calypte costae x *Stellula calliope*[a]	Hartert 1900
Cynanthus latirostris x *Eugenes fulgens*	Short and Phillips 1966
Selasphorus rufus x *Stellula calliope*	Thayer and Bangs 1907
Selasphorus rufus x *Selasphorus sasin*	Newfield 1983

[a] Specimens examined by Banks and Johnson (1961).

on hybridization imposed by interspecific differences in egg volume.

Materials and Methods

For the hybrid diagnosis, we considered the geographic pool (sensu Graves 1990) from which potentially hybridizing species may be drawn to include all hummingbird species (n = 15) that breed regularly north of Mexico or in Baja California del Norte (AOU 1983, see Appendix 1). Neither of the putative hybrid specimens possesses striations or corrugations on the upper rhamphotheca (Ortiz-Crespo 1972), indicating that both birds were "adult." The hybrids (hereafter referred to as "Baja" or "Louisiana" hybrids) were compared with large series of adult males of all North American species of hummingbirds in the National Museum of Natural History (USNM), Smithsonian Institution. Plumage color was evaluated under Examolites (MacBeth Corp.). Measurements of wing chord, lengths of the first (central), third, and fifth rectrices (from point of insertion of central rectrices), greatest widths of the first, third, and fifth rectrices, and bill length (from anterior edge of nasal flange) were made with digital calipers to the nearest 0.1 mm (Table 2). We used bivariate plots of size variables to display morphological variation in two dimensions.

For purposes of the hybrid diagnosis, we used the methodological assumptions outlined by Graves (1990). The hybrid diagnoses followed a two-step procedure. First the presumed parental species of each hybrid were hypothesized through comparative analysis of plumage pattern and color. These hypotheses were then examined with quantitative analyses of external measurements. Concordance of results is regarded as strong support for the presumed parentage of the hybrids (Graves 1990, Graves & Zusi 1990).

Results

Plumage characters.—Neither putative hybrid specimen can be assigned to any known taxon of hummingbird, even after considering the possibility of plumage aberrancy due to mutation or environmental induction. Both specimens possess a distinctive combination of characters that can be found among the assemblage of species in the geographic pool (Appendix 1), but not in a single species, which itself is evidence suggestive of hybridization. Three characters of the hybrids permit their parental species to be identified: (1) a brilliant,

Table 2.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Calypte anna*, *Stellula calliope*, and their male hybrids (MVZ 47983, LSUMZ 154189).

Character	*Calypte anna* (*n* = 12)	*Stellula calliope* (*n* = 12)	Hybrids	
			MVZ	LSUMZ
Wing chord	47.9–51.0	38.0–40.7	44.3	43.6
	49.3 ± 1.0	39.2 ± 0.8		
Bill length	17.4–19.4	13.1–15.1	16.4	16.8
	18.1 ± 0.6	14.0 ± 0.5		
Rectrix 1 length	22.9–26.5	17.5–18.7	21.2	20.0
	24.5 ± 1.0	18.2 ± 0.4		
Rectrix 3 length	26.2–28.5	18.7–20.2	24.5	23.1
	27.6 ± 0.7	19.6 ± 0.6		
Rectrix 5 length	30.3–32.5	18.2–20.3	25.7	25.8
	31.3 ± 0.9	19.3 ± 0.6		
Rectrix 1 width	7.6–10.5	4.1–4.9	5.6	5.7
	8.9 ± 0.8	4.5 ± 0.2		
Rectrix 3 width	5.3–7.4	4.9–5.6	6.1	6.4
	6.4 ± 0.6	5.2 ± 0.2		
Rectrix 5 width	3.0–3.7	3.4–3.8	3.3	3.6
	3.4 ± 0.2	3.6 ± 0.1		

contrasting frontlet; (2) parallel or slightly concave margins of the central rectrices; and (3) rufous margins of rectrices 1, 2, and 3 (Figs. 1–3).

Only two species in the geographic source pool, *Calypte anna* and *C. costae*, have brilliant frontlets that contrast with the remainder of the capital feather tract in color and iridescent intensity (the crown but not the frontlet of *Eugenes fulgens* is brilliant). With the exception of the gorget and frontlet, the plumage color of *C. anna* and

Fig. 1. Lateral view of adult males, from top to bottom: *Stellula calliope; Calypte anna* × *S. calliope* (LSUMZ 154189); *C. anna* × *S. calliope* (MVZ 47983); *C. anna.*

Fig. 2. Ventral view of adult males, from top to bottom: *Stellula calliope; Calypte anna* × *S. calliope* (LSUMZ 154189); *C. anna* × *S. calliope* (MVZ 47983); *C. anna.*

C. costae is similar, but neither species has rufous pigmentation on the rectrices. This means that a species of *Calypte* is a parent of both hybrids, but that neither hybrid could have been produced by an intrageneric union (see Wells et al. 1978).

Adult males of 5 species in the source pool (*Amazilia yucatanensis, Stellula calliope, Selasphorus platycercus, Selasphorus rufus, Selasphorus sasin*) have rufous pigmentation on the rectrices. Of these, only *Stellula calliope* has subspatulate central rectrices with parallel or concave margins (as in the hybrids). Although the Louisiana hybrid superficially resembles *S. platycercus* in gorget color, neither it nor the Baja hybrid exhibits any evidence of the extremely attenuated outermost primary found in males of that species. The hybrids lack extensively rufous or buffy sides, flanks, or rump, as would be expected if *S. rufus* or *S. sasin* were involved (a more detailed description of the plumage is presented in Appendix 2). *Amazilia yucatanensis* can be rejected as a parental species for several reasons, most notably the color of its throat, belly, and fleshy rhamphotheca. Thus, plumage characters suggest that the parentage of both hybrids is *Calypte* sp. × *Stellula calliope.*

Mensural characters.—Assuming additive genetic variance (see Graves 1990, 1996), measurements of the hybrids should fall within the cumulative ranges observed in large samples of the parental species. *Calypte costae* and *S. calliope* are among the smallest species (body mass, wing length) in the geographic pool. Data in Table 2 and values for *C. costae* (Wells et al. 1978), indicate that the length of rectrix 5 of the hybrids exceeds those of *C. costae* and *S. calliope* by a minimum of 12% and 27%, re-

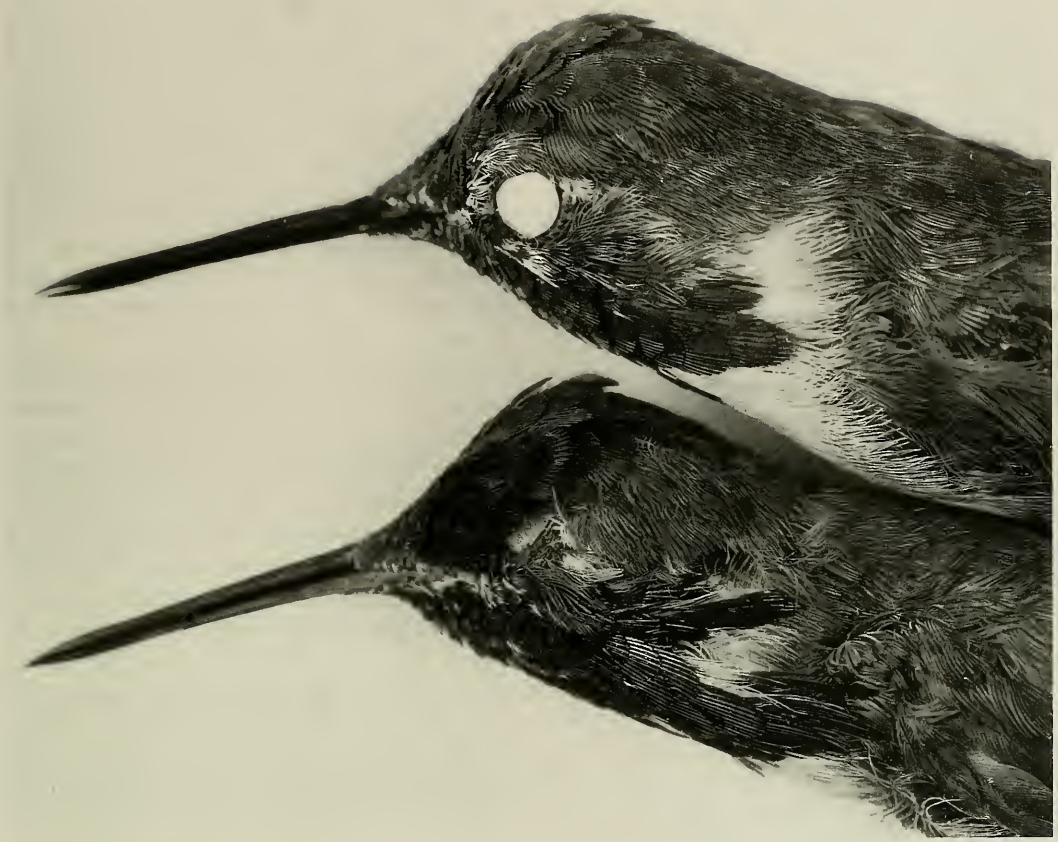

Fig. 3. Lateral view of *Calypte anna* × *Stellula calliope* hybrids: LSUMZ 154189 (top) and MVZ 47983. Note difference in shape of lateral gorget feathers.

spectively. As morphological luxuriance (where a hybrid is larger than either of its parental species) is unknown among trochiline hybrids (Graves, unpubl.), these comparisons effectively rule out *C. costae* as a parental species and suggest that both hybrids are the result of matings between *Stellula calliope* and the larger *C. anna.*

The hybrids are similar in size and shape (Table 2, Fig. 4). Wing, bill, and rectrix length measurements of the hybrids differ from the biparental character means by 0.1 to 6.8%, whereas rectrix width measurements differ by 2.9 to 19.6% from the averages of the character means of the parental species.

Discussion

Field identification of hybrids.—Case histories of the two known *Calypte anna* × *Stellula calliope* hybrids strongly suggest that the parentage of hybrid hummingbirds cannot be determined under field conditions.

Lamb, an experienced field collector, identified the Baja hybrid as "Costa Hummingbird" (*Calypte costae*) in his field catalog. We concur that the hybrid bears more than a superficial resemblance to *C. costae,* particularly in the color and shape of the gorget.

The Louisiana hybrid was studied at close range by experienced observers for

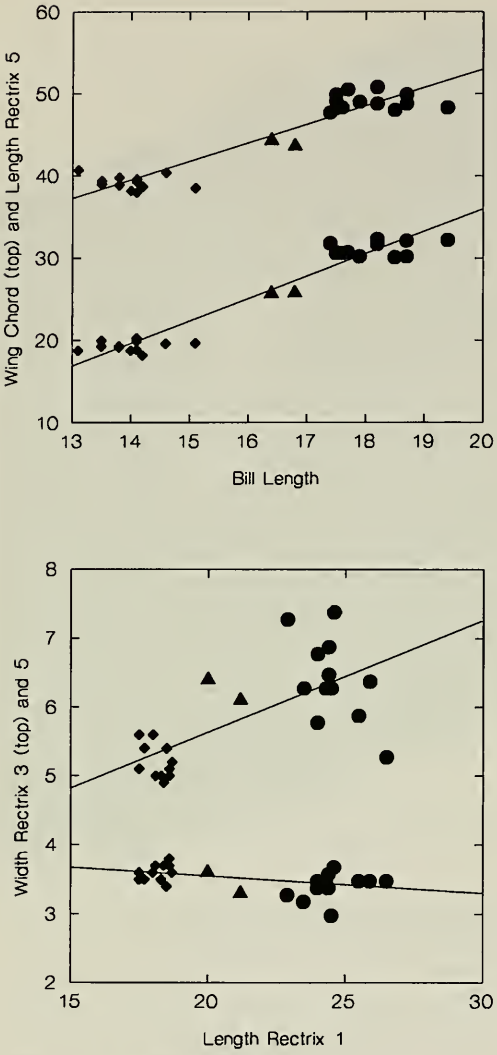

Fig. 4. Bivariate plots of male *Calypte anna* (circles), *Stellula calliope* (diamonds), and their hybrids (triangles, MVZ 47983 and LSUMZ 154189). Least squares regression lines are illustrated for comparison.

several weeks in the vicinity of a nectar feeder before it was collected. The hybrid emitted a high-pitched song similar to that of *C. anna* and loud call notes ("tsick, tsick, tsick . . .") (Paul McKenzie, field notes). McKenzie (19 November 1993, field notes) wrote, "looks more like a Broad-tailed [*Selasphorus platycercus*] in some respects but suggests Anna's [*C. anna*] in others . . . no sign of any reflective feathers on the crown or sides of face . . . [which] should be conspicuous for adult ♂ Anna's . . . cannot see any rufous along the edges of the tail while the bird is perched . . . which would be easily visible for an adult ♂ Broad-tailed . . . the color of the gorget appears more along the shade for Broad-tailed rather than Anna's . . . the shape of the gorget is odd . . . there appears to be a few incomplete feathers on the chin and feathers protrude out on the edges of the gorget . . . almost Costa's like."

McKenzie noted that a second observer saw rufous in the tail, whereas a third believed "the bird to be a typical Anna's." Finally, McKenzie (24 November) reported, "some birders have apparently seen rose-red on the crown and face but I can't see it although (again) the sun is not out." He speculated that the hummingbird might be a hybrid between *C. anna* and *S. platycercus.*

Understandably, none of the field observers suggested the possibility that the hybrid was *C. anna* × *S. calliope.* Subtle shape and color characters that permitted the identification of parental species from specimens would not have been visible on free-living birds, nor could the hybrids have been conclusively diagnosed solely from plucked rectrices or photographs.

Both *C. anna* and *S. calliope* are occasional winter vagrants to the Gulf coast from Texas to Florida (Newfield 1984, unpubl.); perhaps it is not surprising that a hybrid of the two species might occur there as well. However, at least three additional presumed hybrids (*S. rufus* × *S. sasin*) have been collected in this general region in recent years (see Newfield 1983). This seems unusual and suggests an alternative hypothesis that the migratory orientation and behavior of trochiline hybrids is faulty. In other words, the proportion of hybrids may be higher outside the "normal" geographic range of the parental species. Another possibility is that the prevalence of hybrids is geographically invariant, but that hum-

mingbirds are scrutinized more closely in eastern North America.

Are there limits to size differences among hybridizing species?—The body mass ratio (larger divided by smaller) of *Calypte anna* and *Stellula calliope* is approximately 1.6, regardless of which species is female (mass data from Stiles 1971). Although this size difference is striking, the mass ratio is well below the maximum observed among interspecific hybrids of birds (Graves, unpubl.). Mayr and Short (1970) reported a possible hybrid between *Lampornis clemenciae* and *Calypte costae* or possibly *C. anna.* If this combination is correct, the minimum body mass ratio (i.e., ♂ *Calypte costae* × ♀ *Lampornis clemenciae*) would be approximately 2.3 (mass data from Stiles 1971, R. L. Zusi, unpubl.).

This raises the question of paternal effects on avian hybrid viability. Heritability (h^2) of egg size is moderately high in wild birds (Buckley 1982), and the volume of nutritive components of the egg are naturally controlled by the female of a hybridizing pair. In cases in which the smaller of two hybridizing species is female, the egg may not be large enough to support the metabolic and volumetric needs of the developing embryo after factoring in additive genetic effects of the male.

The ratio of average egg volume of *C. anna* and *S. calliope* is approximately 1.2, calculated from the data in Bent (1940). Curiously, however, the range of egg volume for *S. calliope* (ca. 299–611 mm^3) completely overlaps that of the larger *C. anna* (342–591 mm^3) (calculated from the dimensions of size extremes reported in Bent 1940). Thus, despite the specific difference in body mass, egg volume per se appears not to inhibit hybridization between the species. On the other hand, egg volumes of *C. costae* (ca. 276–572 mm^3) and *L. clemenciae* (ca. 662–857 mm^3) are non-overlapping, suggesting that viable hybrids of those species may only be fathered by *C. costae.* Egg volumes of the pairs of hybridizing species listed in Table 1 overlap.

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Appendix 1

Species that regularly breed in Baja California and/or in the United States and Canada: *Cynanthus latirostris, Hylocharis xantusii, Amazilia yucatanensis, Amazilia violiceps, Lampornis clemenciae, Eugenes fulgens, Calothorax lucifer, Archilochus colubris, Archilochus alexandri, Calypte anna, Calypte costae, Stellula calliope, Selasphorus platycercus, Selasphorus rufus, Selasphorus sasin.*

Appendix 2

Comparative description of male *Calypte anna, Stellula calliope,* and their hybrids collected in Baja California (MVZ 47983) and Louisiana (LSUMZ 154189). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason we use general color descriptions.

The forecrown, superciliary, crown, hindneck, back and rump of *calliope* are green with bronzy toning; the loral streak is pale grayish-white. In *anna,* the forecrown, loral region, and crown (anterior from a line drawn across the crown 3–5 mm behind the eye) are feathered with brilliant, iridescent rose-red discs; plumage from the hindneck to the rump is green, slightly bronzier on the hindneck and scapulars than in *calliope.*

In the Baja hybrid, feathers above the nostrils are brownish-gray and dimly reflective (rose-purple) under 10× magnification; iridescent reddish-purple discs extend from the forecrown laterally along the margins of the crown to the rear of the orbits; a few feathers on the crown (between the eyes) are tipped with dull purplish spots. The loral area is buffy-white with dark terminal spots on some feathers. The frontal reflective display in the Baja hybrid is more subdued than in *anna*; the "plate-like" arrangement of barbules of iridescent discs is less well-developed, and several reddish-purple discs exhibit greenish iridescence near the distal margins. The remainder of the crown, hindneck, back, and rump are indistinguishable from *calliope.*

Feathers of the forecrown and crown (to 3 mm behind the eye) of the Louisiana hybrid have terminal discs that emit a dull coppery-rose iridescence when viewed head-on in direct light. The frontal reflective display is less brilliant than in the Baja hybrid (much less so than in *anna*). Under magnification, disc feathers are banded: gray basally, bordered distally in succession by narrow iridescent bands of shining green and reddish-purple merging into a broad terminal band of bronzy- or coppery-rose, with faint greenish reflections. Feathers of the loral area are buffy-white, occasionally tipped with small and indistinct dark spots. Feathers of the hindcrown, back, and rump are green, nearly identical in appearance to *calliope* and most specimens of *anna,* but finely margined with buff, perhaps reflecting the freshness of plumage.

The gorget in *calliope* covers the chin and throat and extends laterally along the sides of the lower throat to form a fringed but tapered point. Gorget feathers are tricolored; proximally white, bordered with a very narrow transitional band of bronzy-green, and broadly tipped with brilliantly iridescent discs (purplish-red).

The purplish-red portions of feathers are greatly elongated in the lateral tails of the gorget. White feather bases result in conspicuous streaking, especially on the center of the throat. A subocular stripe of grayish-buff feathers extends from the loral area to the auriculars. The gorget is bordered posteriorly by a band of white plumage across the lower throat and upper breast. The sides, flanks, and belly are buffy-gray, palest along the midline; feathers on the sides tipped with bronzy-green spots. The undertail coverts are very pale buffy-white or white, some with a few indistinct grayish spots.

The rose-red gorget in *anna* has a similar shape, but the iridescent discs are more imbricated than in *calliope* and extend to the subocular region. Lateral discs are less elongate than in *calliope* and all gorget feathers are dark gray to bronzy-gray basally. Feathers just posterior to the gorget are dull brownish gray with pale gray tips. The remainder of the underparts are dark gray; feathers of the sides, flanks, belly, and undertail coverts have dull bronzy-green subterminal spots. Some males exhibit traces of rosey iridescence on the sides and flanks.

The distribution, shape, and disc color of gorget feathers in the Baja hybrid are intermediate between those of *calliope* and *anna.* Basally, gorget feathers are white or very pale grayish-white, and hence, more like *calliope* than *anna.* A very narrow transitional band of green separates the white base from the terminal purplish-red disc. A buffy-gray subocular stripe separates the eyering from the gorget as in *calliope.* The remainder of the underparts are nearly intermediate to that of *calliope* and *anna.* The throat, immediately adjacent to the gorget, is white, darkening to medium gray on the lower breast, sides, flanks, and belly; feathers on the sides and flanks have green subterminal spots. The undertail coverts (white with a large but nearly imperceptible grayish subterminal spot) are most similar to those of *calliope.*

The gorget of the Louisiana hybrid lacks well-developed lateral extensions observed in *calliope, anna,* and the Baja hybrid, and superficially resembles that of *Selasphorus platycercus* in color and shape. Gorget feathers are pale grayish-white basally (darker near the rachis). A narrow bronzy-green band separates the white feather base from the brilliantly iridescent terminal disc. On most discs, the dominant reflected color varies proximally from coppery purplish-red to coppery rose-red distally. The reddish portions of lateral gorget feathers are not as elongate as those of *calliope, anna,* or the Baja hybrid. White feather bases are visible at the sides of the throat, and especially on the chin and upper throat. The pale grayish-buff subocular stripe is sprinkled with tiny reddish discs; gorget discs extend dorsally to the eyering and auriculars as in *anna.* The gorget is bordered posteriorly by a white band that darkens to light gray on the upper breast and along the midline. Feathers of the sides and flanks have large green subterminal spots and pale buffy margins (especially prevalent on the flanks). The undertail coverts are very pale grayish-white with pale greenish-gray subterminal spots (a few with buffy-white margins), more pronounced than those of *calliope* or the Baja hybrid.

Wing color of *calliope, anna,* and the hybrids is similar. Primary shape in the hybrids is intermediate between that of *calliope* ("squared" primaries 5, 6, 7, and 8) and *anna* (tapered) (see Banks and Johnson 1961).

Rectrices in *calliope* are dull brownish-black with a bronzy sheen, slightly greener on the distal ⅓ of rectrix 1 and 2; the proximal half of the medial and lateral webs of rectrix 1, 2, 3, and 4 (medial web only) are margined with rufous. The central pair of rectrices (1) are semispatulate (web margins proximal to the tip are concave); the margins of rectrix 2 are slightly concave.

Rectrix 1 of *anna* is bright bronzy-green, rectrix 2 is slightly darker. The outer rectrices (3, 4, and 5) are gray along the margins (especially medially), grading to grayish black along the rachis and toward the distal tip. Rectrices lack rufous pigmentation or concave margins.

Shape and pigmentation of rectrices in the hybrids are intermediate between those of *calliope* and *anna.* Overall, the pattern of pigmentation on the rectrices of the Baja hybrid more closely resembles that of *calliope*; the central rectrices are only slightly greener than the outer rectrices, and rufous occurs on the medial (rectrix 1, 2, 3, and 4) and lateral (rectrix 1, 2, and 3) margins. Rectrices of the Louisiana and Baja hybrid are similar, but rectrix 1 and 2 of the Louisiana specimen are greener (approaching the color of *anna*).